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BY B. ARTHUR BENSLEY

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THE HOMOLOGIES OF THE STYLAR CUSPS IN THE UPPER MOLARS OF THE DIDELPHYIDAE

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INTRODUCTION

In the course of my studies on the relationships of the Australian Marsupialia I had occasion to examine the extensive series of skulls of modern Didelphyidae preserved in the British Museum, with the object of defining the ancestral characters present in the dentition. My notes on this subject included a thorough survey of the stylar elements in the upper molars; but, since the main changes in secondary evolution are played upon the main cusps of the molar crown, the modifications of these elements were not referred to in the general results as published,† except where points of sequence seemed to demand their consideration. In fact, the detailed study which I devoted to these structures was undertaken largely through interest in Winge's theory of dental evolution, according to which they are considered as normally three in number and as forming the original elements of the molar crown.‡ It has since appeared to me probable, however, that an account of the modifications of the stylar cusps in such a primitive group as the Didelphyidae would afford a basis for their comparison as molar elements in marsupials with similar structures in placentals, and that possibly their characters might afford a better means of discriminating the molar patterns of early Tertiary or Pretertiary representatives of the two groups than those of the main cusps of the molar crowns, in view of the fact that both are of trituberculate origin. The identification of stem forms depends on the distinction of the primitive characters of marsupials and placentals from one another, and from those which may be common to both; and no adequate conception can be formed concerning them until the habit of denoting the characters of early placentals as "marsupial" rather than as "primitive," or "marsupioplacental" has been finally abandoned.

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* Read at the meeting of the Society of Vertebrate Palaeontologists, New York, December 28th, 1905.

† Bensley, B. A., *On the Evolution of the Australian Marsupialia, etc.* (Trans. Linn. Soc., London; Ser. 2, vol. 9, pp. 83-217.)

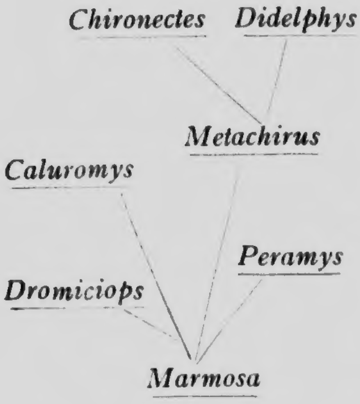
‡ Winge, H., *Om Pattedyrenes Tandskifte, tsaer med Hensyn til Taendernes Firmer.* (Vid. Medd. f. d. Naturh. Foren., Copenhagen, 1882.)

GENERAL CHARACTER AND DISTRIBUTION OF STYLAR CUSPS IN THE EXISTING MARSUPIALS

The stylar elements are accessory structures in the molar crown. They are serially arranged and represent processes of an external ridge or cingulum which passes along the outer faces of the paracone and metacone. They are particularly characteristic of the Didelphyidae, but are found among the Australian marsupials in the Dasyuridae, Peramelidae, and in the phascolarctine division of the Phalangeridae. It is apparent from their associations that they are primitive and more or less conservative elements belonging to the insectivorous stage of evolution. Although reduced in number they are retained in the carnivorous development of the Dasyuridae, two of them being associated with the paracone and metacone in the production of a double shearing edge. In the incipient omnivorous development, as indicated in the Peramelidae, they are retained as in more primitive forms. This is true also, although to a less extent, of the herbivorous and selenodont development as seen in the Phascolarctinae. In the omnivorous and herbivorous developments of the Phalangerinae, in which there is a bunodont modification of the molars, the stylar elements disappear and even in the primitive forms the cingulum is barely indicated. Their function in the insectivorous stage is apparently that of preventing the food from slipping off the smooth concave outer faces of the paracone and metacone, although they are doubtless accessory piercing agents as well. They are associated particularly with the paracone and with the piercing tip of the metacone. The trenchant spur of the metacone tends to be free of these elements on its outer side apparently in order that the shearing action may not be hampered.

THE RELATIONSHIPS OF THE EXISTING DIDELPHYIDAE

In considering the arrangement of the stylar elements in the Didelphyidae it is advisable to bear in mind the probable relationships of the various representatives of the family. These relationships as deduced from a study of the dentition and foot-structure and of other characters are indicated in the appended plan, the details of which are more fully explained in the paper already mentioned (loc. cit. pp. 182-185). The two subgenera *Marmosa* and *Peramys* include the smallest and most primitive forms of the family. They show the closest correspondence in dentition, *Peramys* being if anything the more primitive, as seen in the greater development of the posterior premolar, a character which belongs also to the Oligocene *Peratherium*, judging from the examples which have come to my notice. The subgenera *Chironectes* and *Didelphys*, together with their prototype *Metachirus*, are to be considered apart from *Caluromys* and *Dromiciops*. The former are larger but, in dentition, conservative forms retaining the general conditions of *Marmosa* and *Peramys*, while the latter show special characters indicating the beginnings of omnivorous specialization.



The Stylar Elements in Peratherium

In the estimation of primitive conditions in the stylar formula the question naturally arises—what was the condition of these structures in *Peratherium?* Although through the kindness of Dr. Smith Woodward I was able to examine in detail the British Museum specimens, I was unable to decide this question to my satisfaction. The majority of the specimens represent mandibular rami.* Of the few fragments of upper jaws only one shows the characteristics of the external styles. In this specimen (No. 27807), however, they appear in the molars of the right side in a beautifully preserved, unworn and unbroken condition. They are moderately developed, and present the same condition in m1 and m2. They tend to be reduced in m3, and in m4 they are absent, this tooth being reduced just as in modern Didelphyidae. In m1 and m2 the external cingulum bears in all six elevations, the arrangement of which is shown in the appended diagram of the external profile of m2 of the right side reversed. Three elements, a, b, and c, are conspicuous, and three others, b1, c1, and c2, are subsidiary. Style a is situated at the tip of the anterior spur of the paracone, b opposite its concave face; c is situated opposite the small anterior spur of the metacone. Of the subsidiary styles b1 and c1 are accommodated in the space between styles b and c and appear to be related respectively to these elements. Style c2 is placed on the outer edge of the enlarged metacone spur. This element is so small as to be scarcely recognizable, and its recognition is still more difficult in this specimen on account of the dark colouration assumed in fossilization.

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* Lydekker, R., *British Museum Catalogue of Fossil Mammalia*, pt. 5, pp. 283-288. 1887.

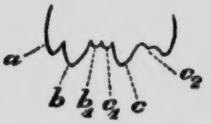

Fig. 1. Stylar Cusps in Peratherium

Apparently the stylar cusps are as well developed in American specimens. Cope* remarks of *Peratherium* that "the superior molars, excepting the last, present two median V's which would be termed external but for the fact that the external basal cingulum is so developed as to constitute an external crest."

THE STYLAR ELEMENTS IN EXISTING DIDELPHYIDAE

Peramys†

P. dimidiata. Two specimens in the British Museum collection show the stylar cusps in an unworn condition, and both

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*Cope, E. D., *Tertiary Vertebrata*, pp. 789 et seq. 1884.

†In this and the succeeding subgenera the descriptions refer only to young specimens or those in which the external styles are quite unworn.

present the same pattern (Fig. 2A—97.1.1.4*). In m1 the elements representing b and c of *Peratherium* are conspicuous. Style a is indicated as a slight projection, and in one of the specimens there is a faint indication of c1. In m2 five projections are shown on the cingular ridge, and these are identical in size and arrangement with those in *Peratherium*, the sole difference being in the absence of c2. In m3 we find again the same condition except that the whole ridge tends to be reduced.

P. scalops. In two specimens m1 and m2 show the absence of the intermediate styles b1 and c1. In m2 the element c2 is present. In m3 style b1 is present in association with c, which is reduced (fig. 2B).

P. iheringi. Two specimens show in all three molars the predominance of b and c, and the presence of both intermediate styles b1 and c1. Style a tends to be reduced, and style c2 is absent; otherwise the pattern is much as in the specimen of *Peratherium* (figs. 1, 2C—61.12.2.9). In m3 the same reduction of the posterior styles is shown as in the specimens of *Peramys scalops*.

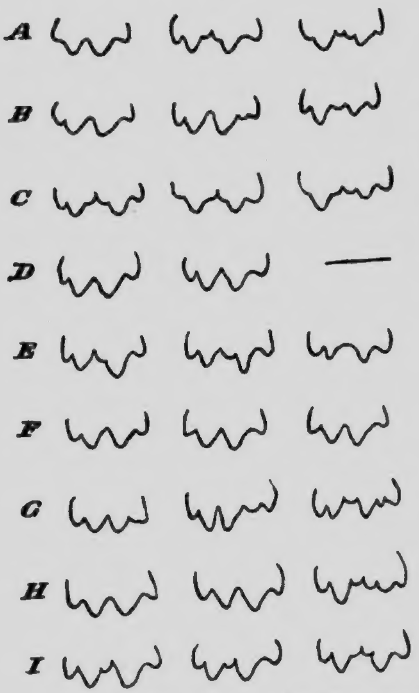

Fig. 2. Stylar Cusps in Peramys

P. sorex. In one young specimen displaying the first two molars the number of styles represents the minimum, only a, b, and c being developed (fig. 2D).

P. americana. In one specimen four elements are present in m1 and m2. Style c1 is seen in association with c, style b1 being absent (fig. 2E). In m3 is shown a reduction of all elements, those present being a, b and c.

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*The numbers indicated are those of the British Museum Catalogue.

P. domestica. Two specimens show in all three molars the minimum of three styles as described for the first two molars of *P. sorex* (fig. 2F—52.2.22.10). A third specimen shows a conspicuous difference. In m2 styles b and c are enlarged and approximated, as generally in the more specialized *Chironectes*, *Didelphys*, and *Metachirus*. Style c2 is present also as in the latter. In m3 styles b and c are separated by an element probably representing c1, but style c2 is still present as a small element (fig. 2G).

P. brevicaudata. Two specimens show the reduced formula in m1 and m2, as in the specimens of *P. sorex* and *P. domestica*. In m3 five elements are present and the posterior ones are reduced, as in the specimens of *P. iheringi* (fig. 2H—0.5.16.60). A third specimen shows practically the same condition except that styles b1 and c1 are only faintly indicated in m3, and style c2 is developed on the posterior face of c. In a fourth specimen m1 and m2 show the presence of style b1 (fig. 2I—67.4.12.540).

Marmosa

M. simonsi. In four specimens the cingular ridge is moderately developed and bears five projections giving a pattern much like the specimen of *Peratherium*, except that the intermediate elements are relatively larger in m1 and m2, and that in m3 style c1 tends to be divided (fig. 3A—99.8.1.23).

M. elegans. In two specimens five elements are again indicated in m2 and m3. In m1 styles a and c1 are more moderately developed and b1 is absent (fig. 3B—98.8.2.12). In five other specimens the intermediate styles b1 and c1 are absent, while in two others the same condition obtains except that c1 is indicated in m3 (fig. 3C).

M. sinaloe. In two specimens only four styles are developed. Of these a, b, and c show their usual relations, while style c1 is in comparison enlarged (fig. 3D). This is a feature which becomes prominent in the species *M. murina* and *M. cinerea*.

M. marica and M. dryus. In three specimens of each species the same conditions are seen as in *M. sinaloe* except that in *M. dryus* style c1 is still better developed and c reduced.

M. microtarsus. One specimen shows the condition of *M. sinaloe* except that in m3 the intermediate styles b1 and c1 are both present as in *M. simonsi*.

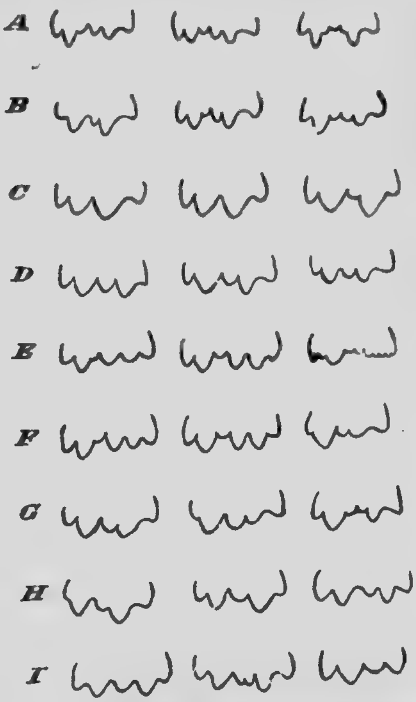

Fig. 3. Stylar Cusps in Marmosa

M. murina. Four specimens show the presence in m1 and m2 of five styles, of which a, b, and c are moderately developed. Style c1 is more definitely enlarged and compares in size with c. Style b1 is barely indicated (fig. 3E, F—97.4.7.12,0.5.1.59). In m3 a different pattern is shown in each specimen. In three of them a, b, and c are indicated, and in two c1 is present (fig. 3F). The fourth specimen shows a more significant arrangement, the cingulum ridge being poorly developed and occupied by a number of low crenulations (eight) prophetic of the condition in the next genus *Caluromys* (figs. 3E, 4B). A fifth specimen shows the increased development of c1 in comparison with c, especially in m2. In m3 the relation is primitive, b1 and c1 being present together and of moderate size (fig. 3G—97.6.7.52). In a sixth specimen a more primitive and moderate development is seen in all three molars (fig. 3H—97.6.7.26).

M. cinerea. The general condition is much as in *M. murina*. In m1 and m2 of one specimen the main stylar elements are b, c1, and c, and these are developed to about an equal extent. Style b1 tends to be slightly cleft. The same three elements are seen in m3, but they decrease from before backwards from b (fig. 3I). In four other specimens the styles are less modified, five elements being typically present, of which b and c show their normal predominance, while b1 and c1 are present together, but of small size. There is a slight reduction of style c in m2.

The relations in *M. murina* and *M. cinerea* are of interest as showing among the variations tendencies on the one hand towards the more primitive condition of the styles, as seen for example in *M. simonsi*, and on the other towards the reduction of the cingulum, as seen in *Caluromys*. The apparent increase of style c1 signifies not an increase in development of the cingulum but a general levelling off of the stylar projections. In the omnivorous and bunodont development of the molars, as seen in the phalangerine division of the Australian Phalangeridae, the cingulum is obliterated, being only seen as a faint ridge in primitive forms. *Caluromys* among the Didelphyidae shows indications of embarking upon this modification, and the two species of *M. murina* and *M. cinerea* which are in many respects prototypal to *Caluromys* show in association with the latter the very first stages in this reduction.

Caluromys

C. laniger. In one specimen the transitional characters between this genus and *M. murina* and *M. cinerea* are well exemplified. In m1 four elements are present projecting to almost the same extent. Particularly noticeable is the increased size of c1 in comparison with c and the absence of b1. In m2 the condition is slightly changed by a peculiar reduction of style b. In m3 the

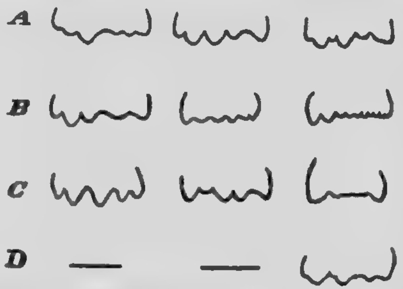

Fig. 4. Stylar Cusps in Caluromys

cingulum is simply crenulated and the individual elements are not apparent (fig. 4C—44.12.18.28). In a second specimen showing the same characters in m1 and m2 the individual elements are apparent, although greatly reduced, and the ridge would still be described as crenulated (fig. 4D—80.5.6.88). In the variety *C. laniger pallida* two specimens show distinctly the reduction of the cingulum (fig. 4A, B—0.7.11.82, 0.7.11.35).

C. trinitatis. Two specimens show minute crenulations only.

Metachirus

The general conditions in this genus and in *Chironectes* and *Didelphys* appear as modifications of those of the primitive species of *Marmosa* and *Peramys*, and it is seen that the development in *Caluromys* is a special one ending as far as the modern Didelphyidae are concerned with that genus. The general arrangement is seen in the approximation of styles b and c, development of style c2, an element scarcely recognizable in the smaller forms, through the shifting forwards of style c, the variable indications of the intermediate styles b1 and c1.

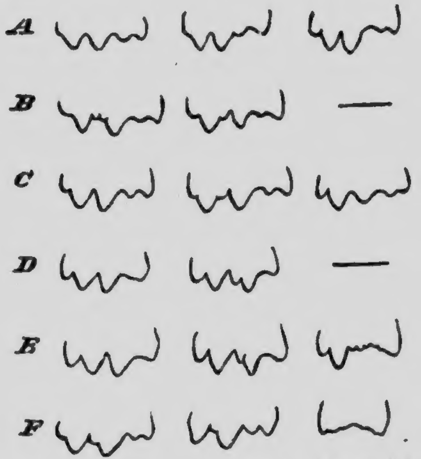

Fig. 5. Stylar Cusps in Metachirus

M. opossum. In one specimen four elements make up the series, namely, a, b, c and c2 (fig. 5A—46.2.2.4). This specimen is abnormal as seen in the development of m4 like the remaining teeth. In m4 styles b and c are present though of small size. A young specimen of *M. opossum var. melanurus* shows the characteristic form of styles b, c, and c2, but the original elements b1 and c1 are present together in m1, definitely showing the homologies (fig. 5B—97.11.7.60). Style b1 is shown in m2 of this specimen and also in a second specimen (fig. 5C—0.7.11.79). In a third specimen it is seen in all three molars. A fourth shows exactly the condition described in the specimen of *M. opossum* in which the intermediate elements are absent in all three molars.

M. crassicaudata. Two specimens show the conditions represented in fig. 5E, F (85.11.26.11, 79.5.1.13), which are easily referable to the general type in *M. opossum*. The cingulum is greatly reduced in m3 in this species.

Chironectes

C. minimus. One specimen shows the approximation and extra development of styles b and c, and style c2 is evident in m1 and m2, so that the type corresponds with that of *Metachirus*. Intermediate styles are absent in this specimen (fig. 6A—849.a), but in a second young specimen they are indicated in m2 (fig. 6B—849.f).

Didelphys

D. marsupialis azarae. The predominance of styles b and c is indicated in two specimens in all three molars, but especially in m1 and m2. In m2 and m3 is shown the presence of two styles posterior to c, probably indicating a division of style c2. In m3 the intermediate b1 is indicated (fig. 6C—84.2.3.25). This element was identified in several specimens. It is sometimes present in the deciduous premolar, which has a molariform pattern.

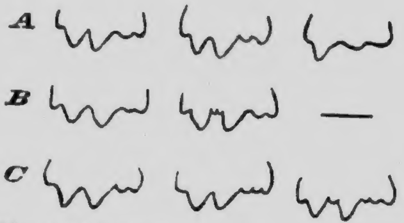

Fig. 6. Stylar Cusps in Chironectes and Didelphys

GENERAL SUMMARY

In comparing the characters of the stylar cusps in an extended series of specimens such as indicated above, three features become apparent. In the first place, as comparatively small and subsidiary structures in the molar crown are certain to exhibit signs of variation, they are surprisingly constant in their relations. Secondly, they show throughout the family indications of a general type, best seen in *Peramys* and *Marmosa*. Thirdly, even in such a poorly differentiated radiation as that represented by the modern Didelphyidae, they show signs of adaptive change. The variations which appear seem to be for the most part significant. The general type indicated is one in which there are three main elements and three more subsidiary ones which I have designated respectively as a, b, c, and b1, c1, c2. If the modern Didelphyidae reflect in the upper molar patterns the primary tri-tuberculate type these main elements are the ones for which homologies must be sought. The general type indicated seems to conform with that described for *Peratherium*, but whether this correspondence would be confirmed on examination of other specimens of *Peratherium* it is not possible to say. That the stylar elements are worthy of consideration in estimating adaptive changes in the molars, or relative specialization, is indicated by Sinclair's* studies on the Santa Cruz marsupials, and my own on the Australian forms. Finally, considering the stylar elements of the modern Didelphyidae as structures not wholly conservative but showing signs of adaptive change and in comparing the family with other, supposedly primitive, forms, the characters presented by *Marmosa* and *Peramys* should be consulted rather than those of the larger specialized forms such as *Didelphys*.

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* Sinclair, W. J., *The Marsupial Fauna of the Santa Cruz Beds.* (Proc. Amer. Phil. Soc., vol. 49, pp. 73-81, 1905.)

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